Occlusal Fingerprint Analysis (OFA) reveals dental occlusal behavior in primate molars

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Introduction

A comprehensive understanding of the occlusal relationship between upper and lower tooth crowns in mammals is essential to interpret the evolution of dental function and adaptations. In fossil species, we can only hypothesize occlusal dynamics based on the analysis of tooth structures, the interpretation of dental macro- and microwear patterns, and the reconstruction of jaw mechanics. We are not able to test and comparably render in vivo details of the chewing physiology and other dental behaviour.

Dental wear patterns are the result of the biomechanical interplay between dental hard tissue, ingested food, incorporated environmental grit, and chemical processes induced by saliva and food itself (Lussi 2002). In this respect it is well known that wear patterns can inform about properties of ingested food materials, and aspects of general environmental setup, such as dust present in the air and adhered to food (Baker et al. 1959, Ungar et al. 1995, Sanson et al. 2007, Lucas et al. 2013). A detailed analysis of dental wear patterns provides evidence about masticatory and para-masticatory occlusal dynamics, based on the upper and lower antagonistic tooth relation during occlusal movements (Butler 1952, Mills 1955). This is of particular interest for the extraction of dietary and behavioural signals encoded in the macro-relief morphology of worn dental surfaces. Since the early 1970s detailed conclusions were drawn from analyses of food composition in the context of macro- and microwear on surfaces of dental crowns (e.g., Crompton & Hiiemäe 1970, Crompton 1971, Butler 1973, Kay 1973, 1975, 1981, Kay & Hiiemäe 1974a, b, Janis 1979, 1984, 1990, Smith 1984). Numerous studies confirmed a distinct correspondence between dental biomechanics, occlusal movements and crown relief structures (M'Kirera & Ungar 2003, Maier 1977a, b, 1978, 1980, Maier & Schneck 1981, 1982, Strait 1993a, b, Teaford 1983, Ungar & Williamson 2000, Ungar & M'Kirera 2003, Ulhaas et al. 2004, 2007).

Biologically, the dentition represents an organismic functional unit for the ingestion and disintegration of food, biomechanically adapted to various food materials (Lucas 2004). Mechanical processes during chewing and other behavioural activities on the tooth surface lead to crown abrasion and attrition (Kay & Hiiemäe 1974a). Consequently, pits and scratches (microwear) emerge on the crown surface, evidencing the loss of hard tissue (enamel/ dentin) due to mechanical stress. The morphogenetic crown relief (primary relief) in a freshly erupted occluding crown is permanently altered (secondary relief) throughout the lifetime of an individual. Physical strain combined with saliva and food-induced chemical erosion results in gradual loss of dental structures on upper and lower crowns in respect to the pattern of sequential antagonistic approaches for the duration of power stroke movements (Fig. 2.1). Tooth-totooth contacts (dental two-body contacts) and tooth-food/ tooth-grit contacts (three-body contacts) (d'Incau et al. 2012) regulate overall mechanical dental wear activities, while the morphology of the antagonistic occlusal surface permanently adapts to individual occlusal dynamics. The contacts occur as integrative effects during repeated dental antagonistic intercuspation, resulting in a recurring precise



Fig. 2.1. The chewing strokes in primate molars. During the power stroke antagonistic tooth contacts may occur. The power stroke is subdivided into an incursive phase (phase I closing stroke) from the first contact until maximum intercuspation, and an excursive phase (phase II opening stroke) until the last contact occurs. Complementary wear facet pairs on the occlusal surfaces of the molars are typically attributed to phase I or phase II movements.

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occlusal fitting of complementary force-fit on the worn surfaces (wear facets = flat and polished enamel areas with well-defined margins created by loss of material) during occlusion (Maier 1978).

The mammalian dentition evolved as a variable and adaptive system, permanently changing functional abilities due to fluctuating environmental and behavioural selective stress for more than 200 million years. Morphological structures of crowns such as cusps, lophs, basins, notches, and fissures determine the major pathways of relief-guided occlusal movements.

Chewing in mammals consists of sequential relatively stereotypic cycles of motion (Maier 1978) operated by a neuromuscular system which is controlled in the brain stem (Luschei & Goodwin 1974, Lund 1976, Luschei & Goldberg 1981, Agrawal et al. 1998). Each chewing cycle (Fig. 2.1) is divided into a sequence of three strokes (Hiiemäe 1978). The opening stroke unlocks upper and lower teeth, and increases the gape of the mouth cavity for food ingestion preparing for the closing stroke, which describes the initial chewing cycle when the lower jaw moves upward until first occlusal contact occurs. That is the moment when the power stroke starts, often divided in two phases (phase I and phase II). In phase I (mandibular incursion) the cusps of the lower and upper molars slide past one another ending up in force-fit individual maximum intercuspation (max $IC \cong$ centric occlusion). Phase II of the power stroke follows when the lower jaw moves out of max IC (mandibular excursion) until the final contact occurs. The molar wear pattern of complementary facet pairs reflects the power stroke only. In phase I of bunodont primate molars the palatinal surfaces of the upper molar cusps contact with the buccal surfaces of lower molar's lingual cusps (Hillson 1996). In phase II the lingual surfaces of buccal lower molar cusps move along the buccal slopes of the lingual upper molar cusps until the antagonists separate (Hillson 1996). Finally, a new chewing cycle starts with the next opening stroke. Kay & Hiiemäe (1974a) described how the system of occlusal wear facets in extant and extinct primate molars develops during repeated power strokes in phase I and phase II applying shearing, crushing and grinding actions to the trapped food particles, while adding saliva to produce a more or less homogeneous and mushy bolus before swallowing.

A number of comparative studies of phase I and phase II macrowear facets have led to numerous labelling systems (Tab. 2.1) for complementary wear facet pairs in upper and lower molars (Butler 1952, Mills 1955, Crompton & Hiiemäe 1970, Crompton 1971, Gingerich 1974, Kay 1977, Maier 1980, Maier & Schneck 1981, Kullmer et al. 2009, Schultz et al. 2018). Typically, the spatial position of wear facets on a molar crown reveals the phase of the power stroke in which they developed (Mills 1955, Butler 1956, 1967, 1973, Kay & Hiiemäe 1974a,b, Kay 1975, 1977, 1978, Grine 1981, Kullmer et al. 2009). Two distinguished sets of wear facets corresponding to phase I and phase II movements are produced in primate molars (Fig. 2.2). Since chewing consists of a number of cycles (Maier 1978) it is favourable to start in max IC as a feasible and definable moment for modelling the pathways of occlusal movements and compare the kinematics of antagonistic tooth contacts (Kullmer et al. 2009, 2012). Max IC has been used as initial position for the concept of the occlusal compass of Homo sapiens molars, sketching latero-, pro-, medio- and retrusive fields of movements for the description of occlusal motion in a horizontal (occlusal) plane (Kordaß & Velden 1996, Douglass & DeVreugd 1997). In addition, surtrusion and detrusion upward and downward occlusal movements (Kordaß & Velden 1996, Douglass & DeVreugd 1997) complement each horizontal movement of the occlusal compass in three dimensions. The dental occlusal compass enables researchers to relate each wear facet pair to an occlusal direction by moving upper or lower crowns out of max IC, while controlling antagonistic contacts (Schulz 2003, 2008, Schulz & Winzen 2004, Kullmer et al. 2009, 2012, 2013, Fiorenza 2009, Fiorenza et al. 2010, 2011 a, b, c). The occlusal compass helps to equate possible directions and tolerance space during an individual power stroke, and for its resulting facet pattern. Even though potential positions of wear facets on the molar crowns are known for most mammalian tooth types, the final detailed appearance of the wear facets, including their size and shape is highly variable and multifactorially influenced. Besides the individual age, environmental and behavioural factors involved, the expression of wear facets depends also on the morphology of the primary relief structures and the exact occlusal relationship of the antagonists (Fiorenza et al. 2010, 2011c, Fiorenza & Kullmer 2013, 2015). Consequently, the individual macrowear pattern,

Crompton & Hiiemäe (1970)	Crompton (1971)	Gingerich (1974)	Kay (1977)	Maier (1980)	Maier & Schneck (1981)	Kullmer et al. (2009)	Schultz et al. 2018
1	2a, 2b	B2	2a, 2b	2	2	F2	ME-d/pr-mb
2	1a, 1b	B1	1a, 1b	1	1	F1	PA-m/pr-db
4	5	B5	5	5	5	F5	PR-ml/md-db
			7	7	7	F7	HY-dl/md-m
		L2	10	10	10	F10	HY-db/pr-ml
			10n	12	12	F12	HY-mb/hyl-l/hy-l
3	3a, 3b	B3	3a, 3b	3	3	F3	PA-dl/hy-mb
6	4a, 4b	B4	4a, 4b	4	4	F4	ME-ml/hy-d
		B7	8, 8n	8	8	F8	HY-I/ed-d
5	6	B6	6	6	6	F6	PR-dl/ed-b
		L1	9	9	9	F9	PR-b/hy-l
			х	11	11	F11	PR-mb/pr-dl
					13	F13	PR-db/hyl-ml
					4'	F2'	ME-ml/hyl-b
	Crompton & Hiiemäe (1970) 1 2 4 3 6 5	Crompton & Hiiemäe (1970) Crompton (1971) 1 2a, 2b 2 1a, 1b 4 5 3 3a, 3b 6 4a, 4b 5 6	Crompton & Hiiemäe (1970) Crompton (1971) Gingerich (1974) 1 2a, 2b B2 2 1a, 1b B1 4 5 B5 2 1a, 3b B3 6 4a, 4b B4 5 6 B6 1 2 1	Crompton & Hiiemäe (1970) Crompton (1971) Gingerich (1974) Kay (1977) 1 2a, 2b B2 2a, 2b 2 1a, 1b B1 1a, 1b 4 5 B5 5 7 L2 10 10n 3 3a, 3b B3 3a, 3b 6 4a, 4b B4 4a, 4b 5 6 B6 6 L1 9 x x	Crompton & Hilemäe (1970)Crompton (1971)Gingerich (1974)Kay (1977)Maier (1980)12a, 2bB22a, 2b221a, 1bB11a, 1b145B555771210101010n12101033a, 3bB33a, 3b364a, 4bB44a, 4b456B6661199x11	$\begin{array}{c c c c c c c c c c c c c c c c c c c $	$\begin{array}{c c c c c c c c c c c c c c c c c c c $

 Table 2.1. List of published comparative occlusal wear facet labelling systems.



Fig. 2.2. Map of buccal phase I, lingual phase I, and phase II wear facets in virtual crown models of *Proconsul africanus* KNM-RU 7290. Upper and lower right M2 in occlusal view aligned in occlusal relationship. The general occlusal compass is oriented for each molar. Major directions of horizontal occlusal movements starting in maximum intercuspation (maximum intercuspation position is indicated by red arrow) are shown by color-coded lines following Kullmer et al. (2009); lateroretrusion (blue), lateroprotrusion (yellow), protrusion (black), medioprotrusion (orange), mediotrusion (green), immediate side shift and retrusion (red). The green-red dashed line in the compass describes the retrusive space. Wear facets are color-coded corresponding to the major directions in the occlusal compass. Each wear facet possesses a complementary facet in the antagonistic tooth. All facets are labelled for comparison. Facets 1 to 4 belong to buccal phase I, 5 to 8 to lingual phase I, and 9 to 13 are identified as phase II facets (Kullmer et al. 2009). No scale.

including the wear facets in their morphometric details, is unique. Therefore, it is described as the occlusal fingerprint of an individual (Kullmer et al. 2009).

The alteration of the occlusal fingerprint of each crown throughout an individual's life represents changing occlusal dynamics from moderate to advanced wear, from a pattern of isolated wear facets towards a single enlarged worn area as a result of merged wear facets in late adult individuals (Smith 1984). With progressive tooth wear dentin is exposed, and dentin basins start to grow until in heavily worn crowns occasionally only a single large dentin

basin, surrounded by a marginal rim of enamel, completely obscures the original wear facet pattern. In most heavily worn crowns the occlusal primary relief has changed into a secondary relief where the remaining enamel surface occurs flat or even concave with a reduced antagonistic indentation, while in crowns with moderate wear the dental articulation is often well-guided by interlocking relief structures along complementary wear facet pairs in upper and lower teeth.

Gradual relief alteration through dental wear indicates changes also in occlusal motion with a gradual increase in the spatial degree of freedom with progressing crown wear. Size, inclination, and inclination direction angles of wear facets inform us about individual three-dimensional occlusal kinematics (Kullmer et al. 2012). A comparison of quantitative wear facet data from large samples in differing and similar wear stages enables us to discuss the variability of the macrowear pattern and dental behaviour for the interpretation of chewing biomechanics, processed food, para-masticatory behaviour, and evolutionary dentofunctional adaptations (e.g. Smith 1984, Kaifu et al. 2003, Fiorenza 2009, Fiorenza et al. 2010, 2011a,b,c, 2015a, 2019a,b, 2020, Fiorenza & Kullmer 2013, Kullmer 2015, Oxilia et al. 2015, Fung et al. 2020).

Those facts inspired us to develop the Occlusal Fingerprint Analysis (OFA) for the quantification and visualization of antagonistic occlusal relationships derived from the analysis of virtual crown surface models. OFA provides a spatial map of the macrowear pattern on tooth crowns, but it also facilitates the size and the three-dimensional orientation of the wear facets, which allows the reconstruction of occlusal kinematics. It records complementary wear facet pairs supporting interpretations of antagonistic approaches during phase I and phase II occlusal movements of the power stroke.

In this chapter, we provide the functional background of quantitative wear facet analyses and the workflow protocol of two principal OFA steps, i.e. the determination and interpretation of the static wear facet pattern in molars, and the virtual simulation and quantification of the sequential occlusal contacts applying the Occlusal Fingerprint Analyser software. Further, we discuss the potential of the OFA approach in respect of specific primate molar adaptations.

Reconstruction of occlusal movements

A satisfactory quantification of macrowear patterns including quantitative assessment of occlusal kinematics from wear facet patterns was for a long time out of reach, although quantitative methods in microwear analyses on wear facets have developed rapidly due to advances in digital microscopy and confocal profilometry (e.g., Kay 1987, Pedreschi et al. 2000, Ungar et al. 2003, Scott et al. 2005, 2006, Schulz et al. 2013, Calandra & Merceron 2016). A few studies focused on the interpretation of microwear pattern for the reconstruction of occlusal movements (e.g. Mills 1955, Ryan 1979, Gordon 1984, Krueger et al. 2008). Many earlier approaches, using cinematography, cineradiography and electromyography (Crompton & Hiiemäe 1970, Hiiemäe & Crompton 1971, Luschei & Goodwin 1974, Herring 1976, Gorniak & Gans 1980) had investigated the general pattern of chewing cycles, but those techniques were not able to visualize occluding dental contacts and wear facets in function with their details at a reasonable resolution. In addition, imaging techniques in those days were mostly limited to two-dimensional visualizations only. The visualization of occlusal kinematics is challenging because occlusion usually occurs in a concealed place within the mouth cavity: cheeks, lips, tongue, food material and saliva surround the teeth, and occlusal contacts are not appropriately assessable (Evans & Fortelius 2008). To overcome this problem Evans & Fortelius (2008) reconstructed jaw movements and occlusion of Recent carnivore species, simulating chewing cycles with virtual dental 3D models. They were able to visualize for example details of the occluding pathway of carnassial tooth pairs in a number of carnivore specimens. They could demonstrate that the carnassials in their sample do not, as expected, describe a linear pathway during vertical occlusal movements. The occlusal trajectories gradually change their angular direction until the crowns reach the max IC, often following concave or convex occlusal pathways. This and other observations would not have been possible without a detailed view on the articulating crown surfaces. They also could show that during the occluding pathway of the carnassial articulation, contacts usually do not occur over a complete facet area in the same moment, but sequentially travel over a facet surface covering just a relatively small facet area at the time. Evans & Fortelius (2008) had to cope with some accuracy limits in their study, including the fact that encountered tooth positions and dental relationship derived from digital scans of dry collection specimens are generally questionable, often requesting precise repositioning of crowns before applying a digital approach. Additionally, at the time of their study the Virtual Reality Modeling Language (VRML) simulation techniques could only handle relatively low-resolution models, which limited the resolution and accuracy on occlusal details.

In the meantime, advances in surface scanning technologies, digital data processing and three-dimensional reconstruction favored the development of new virtual methods for the quantification of occlusion and dental wear facet patterns. Today, the Occlusal Fingerprint Analysis (OFA) determines the size, position and orientation of wear facets in space, and supports the interpretation of occlusal developmental kinematics (Kullmer et al. 2009). Fiorenza (2009) applied the OFA method to a large sample of hominin upper molars, collecting OFA data to determine variability in molar macrowear patterns of Neanderthals and various modern and fossil Homo sapiens hunter-gatherer groups who inhabited different geographic regions. The OFA results showed that the wear facet data contain eco-geographic signals, reflecting dietary preferences and habitat settings (Fiorenza et al. 2011a, 2015a).

A demanding validation of reconstructed trajectories of occlusal movements from OFA data (Kullmer et al. 2009) inspired the programming of a specific OFA software application, the Occlusal Fingerprint Analyser, for reconstruction, visualization and quantitative assessment of sequential antagonistic occlusal approaches, showing that antagonistic contacts on complementary wear facet pairs exist (Benazzi et al. 2011f). Previous occlusal reconstructions of dental movements with no option for a kinematic validation, derived mostly from static considerations of wear facet patterns (Butler 1952, 1973, Mills 1955, Crompton 1971, Kay & Hiiemäe 1974a, Rensberger 1973, Kay 1975, Fortelius 1985), or from simulations with

no real relief guidance (Evans & Fortelius 2008). Now, the OFA software combines 3D simulation by relief-guidance and a contemporaneous recording of area size, position, and spatial orientation of occlusal contacts for functional comparison. The occlusal simulation in the OFA software

integrates the relief-guided motion of crown models derived from collision detection, deviation, and break free algorithms, generating an individual occlusal trajectory, while collecting sequential data from user-defined timesteps of antagonistic colliding dental contacts.

The Occlusal Fingerprint Analysis (OFA)

The recent OFA workflow protocol can be divided in three parts, a qualitative description, the quantification of wear facets, and the reconstruction of the occlusal kinematics.

An OFA analysis usually starts with an investigation and selection of reasonable dental specimens. In this respect it is favourable to work either directly with original specimens, or with high resolution dental casts (Fiorenza et al. 2009). Depending on the specific research question, scholars decide to choose samples in specimens with moderate wear representing fully developed wear facet patterns for most accurate reconstruction of the occlusal pathways, or to use a sample of crowns in various wear stages for studies of occlusal alteration through ontogeny and wear pattern gradients (Grant 1982, Smith 1984, Brown & Chapman 1990, Kullmer et al. 1999, Anders et al. 2011). Ideal for an OFA are usually molars in late wear stage 2 to early wear stage 4 following the categories of Smith (1984). Comparative samples should represent a similar range of wear stages.

An OFA always starts with a macroscopic inspection of the worn crown areas including segmentation of wear facets (Kullmer et al. 2009). An accurate mapping of wear facets and a determination of the number of wear facets is an essential procedure for the study of macrowear pattern and a reconstruction of occlusal kinematic relationship (e.g., Schultz et al. 2018). Initially, the macrowear mapping can be performed in 2D by simply drawing a sketch map of identified wear facets (e.g., Kullmer et al. 2013). Using a binocular microscope usually one can directly identify and draw complementary wear facet pairs (Fig. 2.2), if we work with upper and lower crowns of the same individual by tracing the slightly edged margins of wear facets (e.g., Maier 1977, 1978, Maier & Schneck 1981, Kullmer et al. 2009, 2013). The identification of relative antagonistic occlusal contacts sometimes allows a direct attribution of major directions of occlusal movements for a complementary wear facet pair, if a functional occlusal 3D compass for occlusal articulation, such as it is established for bunodont hominid molars, is known (Kullmer et al. 2009, 2012, 2013). In a wear facet map the individual occlusal fingerprint for a molar or antagonistic tooth pair is visualized (Fig. 2.2). A specific wear facet labelling system combined with a color-code for major directions of occlusal movements helps to standardize the visualisation for qualitative comparisons. The occlusal compass directions starting from the point of max IC in primate molars are divided in protrusion (black), a parallel forward movement of both lower jaw condyles, retrusion (red), a backward motion, laterotrusion (blue), buccal movements, and mediotrusion (green), lingual occlusal motions (Kullmer et al. 2009). In most primate molars we will find combinations of the major directions of movements, such as lateroprotrusion (yellow), lateroretrusion (blue), and medioprotrusion (orange). An occlusal compass can be adapted to any crown morphology.

The collection of presence/absence data, size and spatial orientation of wear facets in a sample of crowns reveals the variability of occlusal patterns. Besides a determination of the occlusal relationship in upper and lower crowns and a reconstruction of dental motion, the occlusal fingerprint can help to enlighten the expression of wear stages, frequency and appearance of malocclusion, as well as para-masticatory use of teeth (Fiorenza 2009, Fiorenza et al., 2011c, 2019a, b, Krueger-Janson et al. 2013, Fiorenza & Kullmer 2013, 2015, 2016). Two-dimensional facet maps derived from investigation of physical tooth surfaces support the determination of wear facets in virtual 3D models (Kullmer et al. 2013).

3D software packages such as Polyworks[™] (Innovmetric Inc.) or Geomagic[™] (Geomagic Inc.) enable a segmentation of wear facets on virtual 3D surface models (Kullmer et al. 2009, Fiorenza et al. 2011a). Virtual triangulated surface models consist of a varying number of connected triangles. Despite challenges in identifying wear facets for segmentation, the model quality of reconstructed relevant functional structures on a crown surface depends on the resolution and accuracy of the raw 3D data (Kullmer 2008). The higher the resolution of a virtual model is, the shorter is the triangle edge length between single data points. A model resolution of ≤0.065 mm is good enough for morpho-functional analysis of dental crowns the size of human molars (Kullmer et al. 2002, 2009, 2012, Ulhaas et al. 2004, 2007, Fiorenza 2010, 2011a,b,c).

A morphometric challenge for functional comparison of dental relief structures and wear facet patterns is the use of a standardized crown orientation, and the comparison of gradually changing wear stages. Classical landmark methods for spatial comparison of shape such as mathematicalstatistical approaches of modern geometric morphometrics (e.g., GMM after Bookstein 1991) including "Procrustes Superimposition" and "Thin Plate Spline Warping" applied for biological shape and size analysis in taxonomical studies of unworn crowns (Weber & Bookstein 2011), or shape comparison of cervical lines of single crowns and jaw bones (Benazzi et al. 2011 a, b, c, d, e), fail in the analyses of functional wear facets. 3D GMM methods are based on spatial comparison of landmarks, semi-landmarks and curves which are likely homologous in sequence and number in a sample. Landmarks can be difficult to define on worn tooth surfaces. Wood & Abbott (1983), Wood (1993) and Ungar et al. (2002) defined on molars a reference plane through the cervix for the morphometry of crown height and crown relief in hominoid molars. The cervical plane is in most wear stages independent of dental tissue loss



Fig. 2.3. Generation of an OFA 3D compass of the wear facet pattern in four steps. **A**, Orientation of virtual 3D model of right M2 (*H. neanderthalensis*, Krapina 137) with cervical standard plane (left), occlusal view (middle), perspective view (right); **B**, (left) 3D model (Krapina 137) in occlusal view with mapped and color-coded wear facet pattern, lateroretrusion wear facets (blue), lateroprotrusion (yellow), mediotrusion (green), medioprotrusion (orange) and tip crushing area (pink), (right) triangulated and segmented occlusal fingerprint, and cut wear facets labelled; **C**, (left) computed best-fit planes of wear facets (Krapina 137), (right) perspective view on best-fit planes of wear facets with normal vectors and cervical reference plane in green; **D**, (left) wear facet vectors (Krapina 137) with normalized length in occlusal view (3D occlusal compass), the shorter the vector appears, the steeper the wear facet, (right) 3D occlusal wear facet compass in perspective view. All images are extracted from Polyworks[™] Modeller and Inspector (Innovmetric Inc.). Not to scale.

through wear (Benazzi et al. 2011c) and therefore it can be used also in most isolated primate molars as standard plane for comparison of functional relief structures (Spears 1994, Spears & Crompton 1996). Kullmer et al. (2002) described the use of a cervical plane and a mesial-distal axis as reference for the spatial orientation of bunodont molar crowns. The cervical plane is calculated in virtual models from a best-fit plane fitted with the least-squares method through a point-cloud of surface data points acquired in a defined distance from a cervical line placed



Fig. 2.4. Wear facet maps and 3D occlusal compasses of six upper right M1 from cercopithecoid species (not to scale). **A**, *Chlorocebus aethiops* (left M1 mirrored); **B**, *Macaca maurus*; **C**, *Papio ursinus*; **D**, *Colobus guereza*; **E**, *Nasalis larvatus*; **F**, *Presbytis cristatus* (left M1 mirrored). All bilophodont molars of Cercopithecidae monkeys show a similar occlusal fingerprint pattern in number of wear facets and the distribution of wear facet directions. But, cercopithecines (A, B, C) with a high fruit content in their diet and more leaf browsing colobines (D, E, F) differ by distinctly steeper wear facets in the latter. No to scale.

manually on the model surface (Fig. 2.3). Afterwards the crown model is virtually rotated in the coordinate system, so that the cervical plane matches the x-y-plane of the coordinate system. In the next step the model is rotated around the z-axis until the mesio-distal axis of the crown is oriented parallel to the x-axis of the coordinate system (Ulhaas et al. 2004, 2007). In this standardized orientation the functional areas such as wear facets in isolated crowns are compared (Kullmer et al. 2009, 2012). This orientation method is also practical for OFA. For functional repositioning of crowns in dental arches scholars choose a standardized occlusal plane for the dentition. Therefore, a plane is fitted through three defined prominent points on the relief of molars and incisors in the dental rows, for example the metaconid cusp tips of the right and left lower second molar, and the incisal point between the edges of the first incisors (Schulz 2003, 2008, Kullmer et al. 2012, 2013). Such an occlusal reference plane is valid also for the reconstruction of the upper dental arch, if the dental relationship in maximum intercuspation with the antagonists is reproducible (Kullmer et al. 2013).

Since the quantification of area size, phase I and phase II area ratio and spatial position of the wear facet patterns (Kullmer et al. 2002, 2009, Fiorenza et al. 2011a) derives from the segmentation of the wear facet on the virtual 3D models (Kullmer 2002, 2009, Ulhaas et al. 2004, 2007), it is important to define the boundary of a wear facet along their slightly edged margins, representing an almost planar, sometimes slightly concave or convex worn enamel surface region. Real edges along wear facet boundaries may develop through a relatively high rate of wear through relief-guidance in occlusal motion with complementary regions in the antagonists. In crown areas with flat slopes such as in basin structures, the facet boundary is frequently obscured, possibly through abrasive polishing of the worn edges (Fig. 2.3).

Preservation of facets does not only depend on the morphology of the relief and the wear stage of a tooth, but also on other factors such as enamel erosion processes, for example due to a high acidity in food and saliva. In those cases, gualitative pre-inspection of the original surfaces, and drawing of a wear facet map, can assist the wear facet segmentation in virtual models. Applying various software tools for visualization such as surface rendering and light source positioning may support wear facet boundary segmentation. Placement of polylines along facet boundaries is the first step of segmentation. Afterwards, re-triangulation of the model with an integration of the polylines into the triangulated grid of the surface model allows a precise selection of all data points within a wear facet for area size determination. The average inclination and direction of inclination of a wear facet can be calculated by using the best-fit plane through all data points of a wear facet (Fig. 2.3). The presence-absence, spatial position, and size of all wear facets describe the occlusal fingerprint of a molar (Kullmer et al. 2009). The occlusal fingerprint can be visualized in classical stereoplot diagrams (Kullmer et al. 2002, Ulhaas et al. 2004, 2007), such as those frequently used in geology and mineralogy for a visual documentation of sedimentary layers or mineral crystal orientation. The stereoplot presentation of wear facets was later slightly refined for easier readability (Kullmer et al. 2009, 2012). Meanwhile normalized vectors for each wear facet are used to represent the spatial facet position in a stereoplot (Figs. 2.3, 2.4). The origin of each facet vector in the stereoplot is placed in the centre of the half sphere and the length of the vector is normalized to the radius length of the sphere. The software module Inspector of Polyworks™ (Innovmetric Inc.) enables a direct generation of wear facet vectors and drawing of the individual 3D occlusal compass (Kullmer et al. 2009). In the stereoplot circle 0° is orientated at the top, indicating the mesial direction of the crown in occlusal view. The steeper the wear facet, the shorter is the vector in occlusal view in a stereoplot diagram of a 3D occlusal compass. It is also possible to turn and orient on screen a 3D compass in perspective view, for example, to explore average inclination and directions of wear facet orientation from buccally, or any other point of view (Kullmer et al. 2009). Facet directionality is readable in relation to the crown orientation and the directions of wear facets can be determined by applying the color code of the general occlusal compass (Schulz, 2003, 2008, Kullmer et al. 2009). The 3D occlusal compass of individual molars represents advancement of the original occlusal compass concept of movements in two dimensions. It enables a comparative visual presentation of individual wear facet orientation (Kullmer 2009, Fiorenza et al. 2010, 2011a,b).

The extraction of wear facet area size attributable to phase I and phase II of the power stroke provides additional functional information. Bunodont primate molars develop two rows of phase I and one row of phase II wear facets in a normal occlusal relationship. Phase I wear facets are divided in buccal phase I wear facets and lingual phase I wear facets. The percentage of size distribution of buccal phase I, lingual phase I, and phase II wear facets allows an interpretation of power stroke portions in phase I and phase II of the occlusal motion. Usually, in molars with a dominance of incursive phase I movements, the wear facets of phase I show an increased surface area compared to the excursive phase II wear facets. The three power stroke proportions are comparably visualized in ternary plots (Fiorenza et al. 2010, 2011a,b).

Occlusal kinematics derived from Occlusal Fingerprint Analysis

Detailed studies of occlusal motion for a more comprehensive understanding of dental articulation and relief guided movements were based for a long time mostly on visual observations from in vivo manual manipulation in patients and volunteers, and handling of physical models in the laboratory. Significant progress was made in modern dentistry, when virtual models were used for the visualization of occlusal distances between upper and lower crowns. Thanks to modern virtual reality applications it is possible to move virtual dental models in the computer along predefined occlusal pathways and record the moment of model surface intrusion (Kordaß & Gärtner 2001, Kordaß et al. 2002, Bisler et al 2002). Meanwhile, digital records of patients' jaw motion are used to simulate natural occlusal jaw movements and dental contacts for dental crown restorations with modern CAD/CAM systems (Solaberrieta 2009).

In the Deutsche Forschungsgemeinschaft (DFG) Research Unit 771 we developed the virtual Occlusal Fingerprint Analyser, a software to digitally establish occlusal contacts and complementary kinematic relationship between wear facet pairs in dental antagonists (Benazzi et al. 2011f, 2012, 2014, Koenigswald et al. 2013, Kullmer et al. 2013, 2015). In the OFA software, two or more 3D models are positioned in a scene window on the computer screen in any arbitrary view. One dental surface model is then moved towards the other along a user-defined rough occlusal pathway, consisting of a number of set path points. As soon as a collision of the models is detected, the moving model is deflected along the surface relief of the other, attempting to reach the next path point. An individual trajectory of relief-guided deflections is generated by calculating the new position of the model per user-defined time steps (Kullmer et al. 2013). The OFA software allows a virtual calculation and simulation of movements with diverse modes for a reconstruction of the potential individual occlusal kinematics. It augments the understanding how wear facet positions and morphology relate to occlusal antagonistic approaches during power stroke motion. The realistic situation of any optional occlusal moment is testable as long as a pair of opposing virtual crowns is aligned in one timestep in a known occlusal position such as the moment of max IC.

There are few requirements of importance to note before working with the OFA software. Two key characteristics of digital surface models are essential to know for using the software application to its full potential. In this respect basic background knowledge about the occurrence of collisions on triangulated surface models, and how collisions can be manipulated, is helpful to evaluate OFA software results. The accuracy of the collision calculation depends on the model resolution and surface roughness in correlation to the software set up of the collision detection distance. A collision is easily detectable as long as the surface model resolution is higher than the defined minimum collision distance. The collision distance needs to be set up by the user in the OFA software, depending on the quality of the virtual models. Almost any triangulated polygon model in Standard Triangle Language (STL) and Polygon File Format (PLY) format can be collided in the OFA software.

At the occurrence of a collision all affected triangles in both surface models are highlighted and recorded. The raw collision data need to be transformed into practical information for occlusal contact comparison. Therefore, the OFA software merges neighbouring colliding polygon triangles into collision groups and quantifies the number of engaged model triangles, area size, and angles of direction and inclination, if a reference plane is setup in the OFA software. The collision groups of triangles are saved for each model together with the resultant trajectory coordinates for each model position per time step of the occlusal sequence. Additional to parallel model approaches, various path point criteria can be set up by the user, including a simulation of rotational lower jaw motion by defining a virtual condyle axis.

In the latest OFA software version (OFA 2.0), more than two models can collide in one OFA project scene. Single tooth models from one dentition can be combined into a trajectory group following the same path, while e.g. recording the dental contacts in complete dental arches in single OFA software projects (Fig. 2.5). In this manner it is also possible to simulate the periodontal motion of each tooth in a dental row in its alveolar socket. When a collision is detected in a trajectory group an evasive movement is calculated depending on the parameter setups of each model in the scene. This allows for a more realistic reconstruction of potential occlusal contacts between opposing tooth crowns. The collision computation can be repeated arbitrarily until model repositioning and the path point adjustment after each calculation lead to a satisfying result in occlusal contacts. Usually this is reached at the moment when the sequential occlusal contacts cover most of the functional wear facet areas during a sequential occlusion.

Trajectory results contain the direction angles of phase I and phase II occlusal movements. This enables a quantitative comparison of occlusal trajectories and the generation of the mastication compass (Koenigswald et al. 2013) based on measured data from occlusal kinematics. The collision data allow a direct comparison of changes in contact area size and position during an occlusal sequence. One can directly follow the contact activity of facet positions during phase I and phase II movements for the discussion of functional aspects and differences in respect to the data of occlusal direction and inclination. The OFA software is freely available on the website of the DFG Research Unit FOR 771 (https://www.for771.uni-bonn.de/for771-en/ofa). In the latest version of the OFA software scholars can display the individual 3D occlusal compass of the dental contact areas of each time step for a direct comparison functional changes during a power stroke sequence.

Perspectives of Occlusal Fingerprint Analysis

Meanwhile, quantitative macrowear analyses using OFA or related methods were applied by scholars initially studying variability and function of wear facet patterns. OFA was used in various modern and fossil mammals in an interand intraspecific context in order to discuss wear facet patterns in molars with respect to evolutionary functional adaptation and dietary ecology (Engel 2005, Huck 2006, Ulhaas 2006, Fiorenza 2009, 2010, Fiorenza et al. 2011a, Schwermann 2015, Menz 2016, Engels & Schultz 2018). Originally, general wear facet analysis was developed to review occlusal concepts established for primate dentitions (Mills 1955, 1963, 1967, 1973, Hiiemäe & Kay 1972, 1973, Kay 1975, 1977, 1978, Kay & Hiiemäe 1974a, Stones 1948, Maier 1977a,b, Maier & Schneck, 1981, Douglass & DeVreugd 1997, Schulz 2003, 2008).

Recent OFA results from a cross-sectional study of primate upper molars in comparable wear stages from more than 40 species of strepsirrhines and haplorrhines show that primate molars vary highly in their phase I buccal, phase I lingual, and phase II proportional distribution of wear facet size (Fig. 2.6).

Some prosimian upper molars without a hypocone, such as molars from Lemuridae or Tarsiidae species, surprisingly possess a relatively high percentage of phase II wear facets compared to species with a hypocone cusp (Menz 2016). The buccolingual slope of the protocone in strepsirrhine species without hypocone is steep and enlarged, usually wear. This is reflected not only in the OFA wear facet data, but also in dental contact data from kinematic OFA in upper and lower molar pairs (Menz 2016). A close inspection on the OFA data of occlusal kinematics reveals that only a very short large antagonistic contact occurs at the phase II facet 9 position towards the end of phase I at maximum intercuspation (Fig. 2.7). In this case, a large facet 9 develops rather from vertical induced crushing activity along steep slopes of the cusps than from a grinding motion as normally expected during phase II through a horizontally dominated occlusal shift. A comparison with the general dietary spectrum of the species (fruits, leaves, insects), demonstrated that strepsirrhini with a high proportion of insects in their diet (e.g., Galago senegalensis, Galago demidoff, Loris tardigradus) possess less phase II wear facet area. This is sometimes the case even if a hypocone is present in their molars, and one would expect an increase in phase II wear. In those cases the facet number can be up to three facets higher than in those species without a hypocone, and the phase II portion is still low. The occlusal sequences and the percentage distribution of phase I and phase II facet areas show a stronger phase I component in insectivorous species than in those with a more variable diet, including a large amount of plant materials. Some insectivorous species (>70 % insects) represent a phase II wear facet proportion of less than 2 %. In those species which are characterized by less insectivorous diet (up to

developing a strong elongated facet 9 with progressing tooth



Fig. 2.5. Screenshot OFA software user-interface. Three open scene windows (dark grey), and collision group window (upper right). OFA project with lower left M1-M3 and P4-M3 single crown 3D models of an Eocene primate (*Cantius ralstoni*, Big Horn Basin, Wyoming). Three antagonistic contacts detected in time-step 18 of the occlusal sequence are visible (yellow), indicated by red arrows in two scene windows in mesiolateral and occlusal view. Scene windows at the lower right shows the normalized vectors of the three detected contact areas in the lower molar row in perspective view (3D occlusal compass of time step). In the collision group window, dip angle and dip direction are displayed for each of the three detected contact areas. Further, the contact area size is provided. All data exportable to comma separated values (CSV) or Excel spreadsheet formats.

35 % insects), the phase II proportion is slightly increased up to almost 9 %. In some species with less insectivorous diet the percentage of the phase II proportion still stays low, even the number of phase II wear facets is increased. This also indicates that if a hypocone is present in some insectivorous strepsirrhines, its phase II wear facets properly do not necessarily enlarge with respect to stronger crushing or grinding activity. This matches the idea that pointed and steep sloped cusps producing steeply inclined facets in insectivorous primates may serve as effective perforation tools to open and cut insect cuticules along small and elongated phase facets (Kay 1975, Maier 1980). It also stimulates a discussion that the invention of a hypocone in molars was maybe not solely coupled with the development of grinding.

Upper molars of *Cantius* species from different stratigraphic levels of the Bighorn basin in Wyoming demonstrate an excellent example in early Eocene euprimates for dental adaptation, and the integration of a hypocone into occlusion (Jones et al. 2014). There is good evidence for parallel environmental and dento-morphological changes during approximately three million years of *Cantius* evolution, but no consensus exists about the dietary preferences of *Cantius* spp. (Gregory 1920, Covert 1986, 1995, Jones et al. 2014). The wear facet pattern of their upper and lower molars and the comparison with those from modern pro-

simians feeding mostly on insects demonstrates that early *Cantius* spp. also retained a low phase II with dominant and steeply inclined buccal phase I facets (Menz 2016).

Even early *Cantius* spp. do not possess a hypocone, such as it is present in modern insectivorous Strepsirrhini; they possess a very similar percentage in the distribution of power stroke phases. In later *Cantius* spp. the hypocone is less pointed and more occlusally integrated. The proportion of phase II facets increases through the development of an additional relatively flat wear facet 10 on the hypocone. This indicates a functional shift in the hypocone which leads together with an increase in tooth size to the assumption that later *Cantius* spp. were more frugivorous. It reflects a timely shift in *Cantius* ecology contemporary to a rise of the average annual temperature in the upper stratigraphic levels of the *Cantius* fossil-bearing deposits (Chew 2009).

There is no doubt that differences in primary morphology between species are expressed in the general appearance of the occlusal fingerprint, since the articulation and indentation of crowns differ (e.g. in depth and position of the antagonistic cusps and basins).

Bilophodont molars of Cercopithecoidea with a welldeveloped hypocone show wear facet areas with a distinct higher percentage of phase II areas than in prosimian monkeys (Fig. 2.6). An increased phase II proportion with two additional wear facets (facet 10 and 11) (Maier 1977b),



Fig. 2.6. Ternary plot of power stroke phase area proportions in primate upper molars. Modern prosimian species in blue, modern cercopithecines with bilophodont molars in green, modern great apes, proconsulids, and *Sivapithecus* in red, and other fossil primates in black.

and the larger size of Cercopithecoidea molars is not only expressed in the larger number of wear facets but also in the wear facet values (Menz 2016). Differences in primary relief height and cusp slope steepness in bilophodont molars of frugivorous cercopithecines versus folivorous colobines (Maier 1977b) are also reflected in the expression of their occlusal fingerprint (Fig. 2.4). Leaf eating colobine monkeys show steeper wear facets at similar wear facet positions than most cercopithecines (Ulhaas et al. 2004).

A very similar development was observed in modern great ape molars with crowns showing the typical Y-pattern fissure pattern of hominids (Engel 2005, Menz 2016, Knight-Sadler & Fiorenza 2017). Gorilla molars with the highest relief produce steeper wear facets than less steep sloped Pongo or Pan molars. Although all of them have a similar background facet pattern consisting of maximum 13 wear facets (Maier & Schneck 1981), the three genera differ in their food spectra. OFA results confirm that dietary ecology of ape and cercopithecine species is recorded in their occlusal fingerprint pattern of the molars. The wear facet inclination in teeth with similar basic morphologies can verify food categories, such as folivory versus frugivory in cercopithecines and great apes. A comparison of the occlusal fingerprint patterns of several species from both groups illustrated some common evolutionary adaptive characteristics in general principles of functional morphology of the wear facet pattern (Fig. 2.6), although basic morphology of the cusp patterns distinctly differs in bilophodont and dryopithecine molar types. Gorilla and colobine monkeys feeding mainly on leaves show very similar functional molar relief with steeply inclined and elongated phase I wear facets, whereas Pongo with its relatively low inclined and enlarged wear facets demonstrates similarities in its OFA results closer to fruit loving cercopithecines (Menz 2016).

Hominoidea molars differ from the bilophodont molars of Cercopithecoidea having a separated hypocone, and usually have a more rhomboid cusp pattern in contrast to a rectangular arrangement of cusp positions in Cercopithecoidea molars. In the upper molars of Hominoidea a new wear facet 13 is formed along the distolingual slope of the crista obliqua (Maier & Schneck 1981), a crest connecting the protocone and the metacone cusps. Functional OFA studies provided new evidence that wear facet 13 develops in the direct neighbourhood of wear facet 12, enhancing the phase II occlusal contacts (Fig. 2.2). This facet was found in only one specimen of the early Old World monkey Aegyptopithecus from the Oligocene, but not in early Cercopithecoidea such as Victoriapithecus from the Middle Miocene (Menz 2016). The OFA data demonstrate an evolutionary shift to a higher variability and an increased phase II compression and grinding capability with the presence of a wear facet 13 in molars of early Hominoidea such as Proconsulidae from the Early and Middle Miocene. In comparison to modern apes, Proconsulidae molars may represent a transitional stage towards a higher compression and grinding capability in later Hominoidea. In modern great apes, Pongo spp. have the lowest relief with relatively flat wear facets and the strongest expression of phase II (Fiorenza et al. 2015b), but we also can find single Pan and Gorilla individuals with a very similar phase II proportion in their occlusal fingerprint (Zanolli et al. 2019). This is also evidenced through a relatively long sequence of contacts during phase II analyzed in OFA data from kinematic analyses (Menz 2016). Upper molars with a dryopithecine cusp pattern display substantial functional differences compared to prosimian monkey teeth, but strongly overlap with monkeys having bilophodont molars (Fig. 2.6).

The comparison of the functional macrowear patterns shows that from the point of split and dichotomous contemporary evolution of the dryopithecine and bilophodont cusp pattern both functional tooth types followed a very similar pattern of functional adaptation. Probably since the end of the Oligocene through the Miocene phase II of the power stroke enhanced. Later bilophodont teeth developed a functional variability mainly in the relief height to cope dominantly with leaves, fruits, and other above-ground growing plant materials. The occlusal fingerprints of great ape molars show that further differentiation with even higher functional variability occurred, probably for dealing with new food resources, i.e. roots and tubers. External food preparation techniques, including cooking, probably has increased the functional variability in hominin molars. The differentiations in wear facet patterns mirror differences in tooth crown architecture, enamel thickness and occlusal dynamics (Schwartz 2000). Further investigations have to clarify, if the hominoid tooth type maybe provides a larger adaptive versatility for variable occlusal pathways than in the strongly interlocking bilophodont teeth of cercopithecines. Studies including OFA data from hominin molars confirm a large variability in the facet pattern (Engel 2005, Huck 2006, Ulhaas et al. 2007, Fiorenza 2009), highlighting also basic differences in the wear facet pattern between great apes and hominins in particular in the distribution of area size distribution in context of the power stroke phases (Zanolli et al. 2019). This still needs to be investigated in more detail.

The comparison of molar wear facet patterns in Late Pleistocene Homo sapiens and Homo neanderthalensis underlines the observations of a high diversity within the genus Homo (Fiorenza 2009, Fiorenza et al. 2011a). H. sapiens hunter-gatherer and early agriculturalist groups exhibit a high variability in inclination and direction of inclination in wear facets (Fiorenza et al. 2009, Fiorenza et al. 2018). OFA data on wear facet size proportions and inclination also illustrate that cultural evolution with the invention of and increasing versatility in preparation of foods reflect a higher food choice mirrored in the functional adaption of the macrowear pattern in Homo (Fiorenza et al. 2011c). Wear facet patterns of molars from H. sapiens of hunter-gatherer groups with known food spectra match with H. neanderthalensis samples from similar eco-geographic regions and time intervals (Fiorenza et al. 2011c). Molars from groups that lived in temperate and cooler conifer-forest environments in Central Europe are distinguishable in their occlusal fingerprint from groups that thrived in evergreen deciduous forests in the Mediterranean areas (Fiorenza et al. 2011c). Relative steep buccal phase I wear facets occur in fossil H. sapiens. Neanderthals. and modern hunter-gatherers. such as Inuit and Vancouver Islanders feeding generally on a diet rich in meat with a low plant contribution. In contrast, a high portion of plant foods obviously promotes the preparation of larger lingual phase I wear facets such as it was reported in Australian aborigines and African bushmen as examples of mixed-feeders. Some simple functional considerations may support these observations. More rough, fibrous and tough meat probably is easier to chew with a strong, vertical and relief guided bite producing dominant edge contacts along steep buccal phase I shearing facets. Harder and brittle plant food is better crushed and ground with powerful high pressure in vertical and lateral occlusal movement. This is expressed in flat buccal phase I wear facets and the integration of increased lingual phase I and enlarged phase II wear facet areas (Fiorenza et al. 2011c). Neanderthals from steppe and coniferous forests of Central and Eastern Europe show the lowest variability in their wear facet patterns, with large and relatively steep buccal phase I facets, very similar to meat-eating Inuit and Vancouver Islanders. Neanderthal groups from warmer deciduous forest and evergreen habitats are similar in their phase I wear facet area distribution to the mix-feeding attributed to bushmen and Australian aborigines. In both fossil groups, Neanderthals and Pleistocene *H. sapiens*, the significant differences can be assigned to differences in ecogeographic habitats and nutrition strategies.

Previous OFA results of hominoid molars emphasize that ecological factors (for example climate and vegetation) which are to be interpreted in connection with the existing food resources are manifested in the expression of specific occlusal tooth contact patterns. These can be understood as variants of the general wear facet pattern as described by Maier & Schneck (1981). Considering the evolutionary development of the general pattern of tooth contact surfaces in the bunodont hominid molars as a function morphological adaptation (Maier & Schneck 1981), the specific expression of the contact facets can be regarded as a functional reaction of the tooth construction. Teaford & Ungar (2000) and Ungar et al. (2006) summarized the ecological adaptation of hominid tooth construction in tooth size, crown shape, enamel structure, enamel thickness, and general biomechanics as an example of a flexible adaptation to the environment and cultural development. The extent to which the ontogenetic variability and the different variants of contact facet pattern reflect dietary flexibility of a primary construction can only be understood, if the function of wear facets is apprehended in the context of biomechanics of the entire mastication system. The comparison of the absolute and relative wear facet areas with the cusp area and cusp height of the most discriminating cusp (hypocone) in H. sapiens and Neanderthal molars shows that the primary morphology of the cusps has little effect on wear facet size (Fiorenza et al. 2011a), and the appearance of large wear facets and their leveling depends essentially on environmental factors (habitat, climate, food resources), finally triggering chewing and cultural behavior. However, it is confirmed that the development of the general wear facet pattern of hominoid molars is closely related to the primary morphology of tooth relief and occlusal jaw movement (Kullmer et al. 2012). The experimental simulation of the occlusal movement confirms a direct correspondence of the movement space described in the dental occlusal compass with the emergence of the wear facet patterns (Kullmer et al. 2012). Deviations in the space of movement, e.g. because of chewing different diets, leads to changes in the shape and absolute position of the wear facets (Fiorenza et al. 2011a). Variations in the inclination direction of the facets are therefore attributable to differences in the movement pattern (Kullmer et al. 2012). The presence of a complete hominoid wear facet pattern (facets 1-13) on a molar depends not only on the presence of all cusps and the occlusal relationship, but also on the wear stage of the tooth, and on the molar position (Fiorenza et al. 2010, 2011a). Only when the tooth is erupted and in occlusion, the contact facet pattern develops. In the case of the first and second permanent molars (M1 and M2), a complete pattern with 13 facet positions is established



Fig. 2.7. Comparative OFA visualization of an insectivore (*Loris tardigradus*) and a fruit and leaf eating (*Lemur mongoz*) strepsirhine primate right M1. From left, 3D model with wear facet map in occlusal view, 3D occlusal compass, sequential power stroke contact area size kinematics and mastication compass with phase I (blue) and phase II (green). Not to scale.

during normal occlusal relationships (Ulhaas et al. 2007, Kullmer et al 2009, 2012).

In OFA of upper third molars (M3) it was found (Fiorenza et al. 2010) that facets 7 and 10 are absent in the fully formed pattern in H. sapiens and Neanderthals, since the upper M3 distally contacts with the lower m3 only. Therefore, there are no antagonistic crown surfaces present in the mandibular dentition for positions 7 and 10 at the distal slope of the hypocone (Fiorenza et al. 2010). The OFA results and wear facet map may thus be helpful in the determination of isolated third molars. This was the case with the Neanderthal tooth D58 from Krapina in Croatia (Fiorenza et al. 2010), where the OFA results could identify the crown as a third molar underlined by its reduced hypocone and a missing distal interproximal contact facet. Distally, the molar has distinct facets 7 and 10 whose inclination direction and angle of inclination indicate that, in addition to its direct antagonist in the lower jaw, there were also two contacts to a more distally positioned opposing tooth, and therefore it should be rather identified as an upper M2 than an M3 (Fiorenza et al. 2010). Taking into account the principles of intercuspation of the molars, it is possible to determine the exact positional relationship of the antagonists via the occlusal fingerprint pattern (Kullmer et al. 2013).

If the antagonists are available, the determination of the angles of the facets (inclination direction and inclination angle) in the 3D occlusal compass for both teeth can be established and the correspondence of the complementary patterns can be quantitatively demonstrated (Kullmer et al. 2012). Thus, the tooth position of the premolars as well as M1 and M2 can be verified. The assessment of facet correspondence not only gives an objective evaluation of the

association of isolated teeth (Fiorenza et al. 2010, Kullmer et al. 2012), but it can also be used for evidence of paramasticatory activity, such as the use of the teeth as a third hand for holding and manipulating objects (Fiorenza et al. 2011b). In addition, the identification of facet patterns and OFA data is important for the most realistic functional repositioning of dental crowns in the dental arch (Kullmer et al. 2013, Benazzi et al. 2013a). This is of particular relevance for the reconstruction of the occlusal mechanics and the comparison of the chewing motion of rows of teeth and complete dental arches. Despite the numerous studies on the occlusal relationship of tooth contacts in primates (Mills 1955, 1963, Hiiemäe & Kay 1973, Kay 1975, 1977, 1978, 1981, Kay & Hiiemäe 1974, Stones 1948, Maier 1977a, b, Maier & Schneck 1981), the quantitative OFA data and the occlusal 3D compass (Kullmer et al. 2009) offer for the first time the possibility to directly compare and visualize the multiple facet patterns of teeth in a standardized diagram (Fiorenza et al. 2010, 2011a,b, Kullmer et al. 2012).

A comparative diagram for occlusal trajectories has also been missing. Inspired by the 3D occlusal compass, Koenigswald et al. (2013) proposed a new terminology and visualization of the occlusal pathways in mammalian molars based on the spatial orientation of wear facets and of "microwear" striations on the tooth surfaces (Fig. 2.7). The mastication compass combines the number of movements during the occlusal phases, the direction and the inclination of each individual phase into a three-dimensional overall movement pattern of the "power stroke" in a single diagram (Koenigswald et al. 2013). An overview comparison of mastication compasses from different mammalian molars in a wear stage with full wear facet development shows the enormous variability in power stroke movements as a function of the different crown shapes. In most bilophodont and secodont molars, the incursive phase I is very dominant. Examples of such dentitions are found in arvicolids, elephantids, and modern Equidae. In lophodont, selenodont, and secodont teeth with a high relief, the movement is clearly guided in comparison to relatively flat bunodont teeth. It remains unclear whether mammalian mastication is actually controlled by the composition and quality of food or by phylogenetic preconditioning (Koenigswald et al. 2013). Initial observations in different mammals suggest that high quality (high energy) food correlates with a prominent phase I during the power stroke seen in many insectivorous and carnivorous mammals, and the combination of phase I and phase II is apparently appropriate, if a larger amount of slightly less energetic food is on the menu, such as in Proboscidea, Ruminantia, Equidae and some Rodentia (Koenigswald et al. 2013). The connection of two phases can lead to synchronization in the direction of movements when comminuting very low energy food. In the biphasic bunodont teeth of hominoids, a large variability in occlusal motions is demonstrated by a large variability in the OFA patterns (e.g., Fiorenza et al. 2011c). Here it turns out that particularly bunodont dentitions of hominoids can react within their construction and show the possibility of adaptations of motion in their wear facet patterns to variable foods.

In order to be able to show the correlation between a flexible chewing behavior and the adaptation in the primate masticatory apparatus, it is important to reconstruct the occlusal trajectories in complete rows of teeth. A precise 3D mapping of the wear facet positions and the measurement of the spatial facet directions (OFA), in the sense of the dental 3D compass, provides the methodological prerequisite for quantitatively detecting the correspondence in the occlusal movement pattern and tooth wear in primate teeth and complete tooth rows. Beyond doubt, the positions of the antagonistic wear facets of hominoid molars show occlusal contacts during the occlusal power stroke and in maximum intercuspation in a natural dentition on both sides of the dental arch. In dentistry, one speaks of a balanced occlusion (Douglass & DeVreugd 1997, Schulz 2008). In many anisognatic mammalian tooth systems (e.g., Bovidae, Cervidae, Equidae, many Rodentia), there is no or only a partially balanced occlusion, as we can see it in most prosimians with an unfused symphysis.

This does not necessarily mean that bilateral chewing predominates in hominoid dentitions, but it is rather possible due to the fact that it does not produce contact interferences during chewing on the respective working side. This is observable in a perfect functional interplay of the phase I wear facets on one side and the phase II wear facets on the other side of the jaw. The documentation of the occlusal fingerprint in complete crown rows of hominoid individuals (Kullmer et al. 2013) and physical testing with dental models in natural rows of teeth, show that the spatial position of phase I wear facets on one side coincides with the alignment of the wear facets of phase II on the opposite side in the occlusal motion. This can be explained also by the translation and rotation in the two condyles of the joints during the "power stroke" (Kullmer et al. 2012, 2013). However, it is still debated at what exact time of the occlusion the phase II facets actually arise (Wall et al. 2006). The two-sided sliding over the tooth surfaces during the occlusion supports as precisely as possible a functional reconstruction of the occlusal movement of complete dental arches of hominoid individuals. Thus, through the functional understanding of individual wear facet relations, derived from OFA, the complete dentition of a specimen of the Miocene ape Rudapithecus hungaricus from Rudabánya could be restored. The occlusion has been functionally tested in a physical model in a dental articulator, and in parallel with virtual 3D models in the OFA software (Kullmer et al. 2013). The occlusal fingerprint of the individual shows a good fit of the occlusal contacts and leaves almost no room for variation in the positioning of the molars. The static and kinematic occlusion was first qualitatively assessed with the physical models in a dental articulator, a device commonly used in dental laboratories. A quantitative evaluation of the reconstruction was made by virtual measurement of the tooth contacts after repositioning. The comparison of the wear facet pattern with the contacts in the static occlusion was carried out by a virtual surface distance measurement of the maxillary and mandibular arch in the maximum intercuspation. The pattern of the minimal distances (<0.1 mm) of both models in comparison with the facet pattern reflects the precision of the interlocking in the dentition of the young adult Rudapithecus individual (Kullmer et al. 2013). An examination of the kinematic occlusion was carried out with the OFA software by means of relief-guided collision detection. Thus, it could be shown with the virtual motion simulation, and the detection of the tooth contacts, that during the sequential occlusion of the reconstructed mandibular arch there is no interference in the occlusal jaw movement. Such a functional dental arch reconstruction was first performed with Rudapithecus, and it provided a functional basis with a well articulating dentition for a full skull reconstruction of the fossil specimen (Gunz et al. 2020), such as it was put into practice with the Australopithecus africanus specimen Sts 52 (Benazzi et al. 2013a). A review of the trajectory of the occlusal sequence from the virtual OFA simulation in Rudapithecus indicates that the bite of the individual at this stage of tooth wear was characterized by a prominent incursion from buccally with a strong vertical movement. After minimal lingual translation of the lower jaw during phase II the crowns separate rapidly, guite similar as it can be observed in young gorilla individuals, feeding on young juicy soft plant shoots and fruits (Kullmer et al. 2013).

Computer simulation and virtual motion analysis in combination with OFA data is still in its infancy, but it can already be predicted that virtual 3D crown morphometry in combination with virtual motion concepts fundamentally expands the functional analysis of dentitions. The OFA analysis with its quantitative possibilities of wear facet patterns with the reconstruction of the occlusal trajectories allows the study of entire occlusal kinematic patterns of the mastication system in its complex mechanical context of food comminution.

In the latest version of the OFA software (OFA 2.0) scholars can consider the temporomandibular joint geometry and also the movement of single teeth in their alveolar socket for a more realistic simulation of real occlusal. Future

software versions should incorporate simulations of food particles over the occlusal surfaces, to quantitatively study crushing and shearing performance.

In the meantime, results from kinematics analysis of the occlusion are incorporated in simulations of the occlusion dynamics, including dental loading scenarios. The aim is to test effects of occlusal motion patterns and tooth wear pattern on force reaction patterns and adaptations in the 3D structures of the masticatory system. First results from combination of OFA and finite element analyses (FEA) were drawn from H. sapiens molar pairs (Benazzi et al. 2011f, 2012, 2016). Based on individual occlusal movement contacts on lower first molars of two individuals in two different stages of wear, the distribution of the loads in the tooth and jaw bone at different moments of occlusion was compared for the first time. From microcomputed tomography data of teeth and jawbones, different tissues in the tooth crown structure were segmented for a numerical computation of loading scenarios. Finite element models for enamel, dentin, cementum, pulp, periodontium, and compact and spongy jawbone were calculated and brought together in an overall model for the application of occlusal force (Benazzi et al. 2011f). After the physical properties (data from literature) were assigned to each tooth material, the strain vectors for the tooth contact areas, from data of time steps of the motion simulation with the OFA software, were calculated as resulting vectors. The occlusal load was calculated during three occlusal contact moments: (1) initial occlusion (phase I), (2) maximal intercuspation, and (3) in the excursive phase (phase II). The pattern of stress distribution in the dental bone system showed significant differences in tensile stress distribution as a function of the occlusal position, especially in the cervical region of the crown, at the enamel-dentin junction, in the fissure pattern, and in the roots (Benazzi et al. 2011 f, 2012).

This was the first FEA applying an individual loading simulation derived from OFA kinematic results in a complex FEA tooth model. Principal stresses were observed along the fissures of the tooth surface and in the crown walls (Benazzi et al. 2011f). Contrary to previous studies in unworn *H. sapiens* molars, the highest tension in worn tooth crowns with wear facets occurred cervically at the mesial and distal walls rather than buccally or lingually as previously assumed (Benazzi et al. 2011f). This suggests that facet patterns can contribute to a more favourable distribution of occlusal forces due to their enlargement and flattening of the contact areas, whereby pits and fissures are critical localities, since a concentration of tensile stress takes place there, as recently underlined through a study with premolars (Benazzi et al. 2013b). This also suggests that the fissures with their profiles and varying enamel thickness contribute to the general stiffening of the crown. Similarly, it could also be related to the functionality of the mid-trigonid crest, an edge structure connecting metaconid and protoconid (Benazzi et al. 2013b). This structure is also found in most Neanderthal molars while it lacks, or is only very weakly developed, in H. sapiens.

Conspicuous tensile stress occurred in the bifurcation of the roots at maximum intercuspation. This is maybe an indication for adaptive occurrences of a strong expression of taurodontism with a shift of the bifurcation in Neanderthals, who were interpreted to have produced higher loads in their pointed face (Trinkaus 1987, Benazzi et al. 2015). Probably, an apical displacement of the root separation and also root fusion can contribute to a reduction of tensile stress in the roots at maximum intercuspation (Benazzi et al. 2013b). An increase in facet size and a flatter inclination in the advanced worn tooth crowns results in a more tooth-axis-oriented distribution of forces so that the buccal and mesial cervical margins are less conspicuously stressed. This load image provides e.g., a relatively simple explanation for the frequent occurrence of cervical enamel chipping at the buccal enamel margins of human teeth in modern industrialized societies. We have critically reduced natural tooth wear as a result of eco- and socioesthetical behaviours. The abridged masticatory activity due to externally processed and softened food, as well as a prolongation of the individual longevity may contribute to common fatigue in enamel and dentin observed in modern H. sapiens, resulting in an overload reaction in the dental crowns in the cervix area towards tooth and root fractures (Benazzi et al. 2013b). Stress distribution patterns from premolars with crowns in various wear stages provide a simple biomechanical explanation for the frequent occurrence of cervical enamel chipping (non-carious cervical lesions) at the buccal enamel margins in humans from industrialized societies.

The results from previous studies of virtual OFA describe an innovative approach to capture relevant functional structures for the reconstruction and visualization of occlusion and structural adaptation in teeth. The acquisition and data processing of three-dimensional structural data still require a relatively large amount of time, making it difficult to evaluate larger samples. It will be a major endeavour for the future to shorten time for OFA data acquisition by an intensive work on the automation of OFA processes. A larger throughput of sample quantities will significantly enhance OFA applications. Nevertheless, OFA methods are useful to simulate and compare evolutionary developments in tooth structures and to evaluate their adaptive effect. A future challenge in functional analysis of dental structures will be to experimentally validate results from virtual biomechanical simulations such as FEA.

OFA offers a range of innovative methods that contribute to a comprehensive paleobiological understanding of functional relationship between tooth structures and occlusal biomechanics, and evolutionary dental adaptations and behaviour. OFA studies on hominid molars including H. sa*piens* are closely related to societal applications in modern dentistry (e.g., prosthodontics, orthodontics, implantology) but also nutritional sciences, and they are maybe also supportive for other disciplines in human medicine. From an evolutionary perspective, OFA can provide important quantitative data to understand the increase in modern occlusal dysfunctions, temporomandibular joint problems, and possibly even digestive disorders, occurring frequently in modern industrialized societies. Some of them may be closely related to dietary behaviour and the consequent reduction of use in our masticatory system in its original biological sense.

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